DIFFERENTIAL MORTALITY AND RELATIVE MATERNAL INVESTMENT IN DIFFERENT LIFE STAGES IN *STEGODYPHUS LINEATUS* (ARANEAE, ERESIDAE)

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ABSTRACT.   The general reproductive pattern in spiders is to produce large clutches with small eggs although some species produce a few, large eggs. The spider *Stegodyphus lineatus* (Eresidae) is unusual in that it lays a single extremely small clutch and has small eggs. The female feeds the young after hatching and eventually the young completely consume her.

Differential mortality risks in different life stages may provide an explanation of relative maternal investment in eggs *versus* hatchlings. By monitoring natural populations of *S. lineatus*, sources and rates of mortality were assessed during the reproductive period. Complete failure of reproduction was more likely during egg development than after the spiderlings had hatched. This was partially explained by the presence of a parasitoid wasp that only attacked females before the young had hatched. Overall attack rates were similiar in the egg stage and in the hatchling stage; however, the spiderlings suffered less mortality because they were mobile.

By allocating the major reproductive effort to hatchlings rather than eggs, these spiders may pass through the risky egg stage relatively fast; and overall development and growth can be maximized. Small egg size might be an adaptation to high predation pressure during the reproductive period. Small clutch size can be explained by the importance of early growth for offspring fitness.

Parental care is considered to increase the survival probability, and often the reproductive value, of offspring (Clutton-Brock 1991). Accordingly, parental care is usually associated with a high investment per individual young (Shine 1978; Sargent et al. 1987; Stearns 1992). Assuming that a female has a limited amount of energy to invest in reproduction, an increase in investment per individual young will reduce the number of offspring that can be produced. Thus one may expect that animals with brood care will have relatively few but large offspring. This is indeed the case in many oviparous ectotherms, where the amount of parental care and propagule size are positively correlated (Shine 1978; Gross & Sargent 1985; Sargent et al. 1987; Clutton-Brock 1991; Roff 1992).

Large propagules can be achieved in two different ways: resources can be invested in offspring either by providing them with yolk at the egg stage or enhancing growth by feed-ing the young after hatching. The first form of resource allocation is the more common one in oviparous ectotherms in which parental care is mostly egg guarding and is associated with relatively large eggs (Shine 1978). However, extended brood care does occur in many species; and differences in the allocation of resources into the various developmental phases may be a result of different predation pressures in the different stages, with selection pressures similar to those proposed for the evolution of egg size *per se* (Shine 1978, Sargent et al. 1987). In the "safe-harbor" hypothesis, Shine (1978) proposed that in oviparous ectotherms that large eggs should evolve if predation pressure is high during the juvenile stage, and small eggs should be selected for if mortality is relatively high in the egg stage.

In many species, total clutch mass is a function of female body mass (Craig 1987; Anderson 1990; Marshall & Gittleman 1994). Variation in clutch mass mostly results from differences in clutch size rather than in egg size (Marshall & Gittleman 1994). Most spiders lay several large clutches with small eggs

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and die before the young hatch (Foelix 1981; Marshall & Gittleman 1994). The parental care they exhibit is to spin silken cocoons around the eggs and to position these cocoons in places where access for predators is difficult. Some spiders guard their egg sacs and may carry their young after hatching. After correcting for female body size, Simpson (1995) found no difference in clutch size nor in egg size between spider genera that guard eggs and carry young and those genera that provide less or no parental care. Simpson (1995) concluded that female size, and not the type of parental care, is the primary factor that influences clutch and egg size in spiders. Extended maternal care that includes the feeding of young is less common in spiders and has not been included in comparative studies of egg and clutch size.

The eresid spider, *Stegodyphus lineatus* Latreille 1817, is unusual in that females produce small clutches with small eggs and also exhibit extended maternal care. The average clutch mass represents only 2–3% of the female's body mass which is an extraordinarily small investment in eggs (see Marshall & Gittleman 1994, the smallest female mass/clutch mass ratio in a sample of 40 species is 16%). Other spider species of a similar body mass of 200–500 mg lay several hundreds of eggs (Marshall & Gittleman 1994); *S. lineatus* lays only about 70. Instead, *S. lineatus* females invest all their remaining resources into the spiderlings after they hatch. Females release the spiderlings from the egg sac and feed them via regurgitation. The young consume their mother's entire body content, and she dies about two weeks after the young hatch. Consequently, juveniles disperse at a relatively large size. Similar forms of maternal care, involving provision of food for the young, have evolved in at least six spider families: Agelenidae, Amaurobiidae, Eresidae, Heteropodidae, Theridiidae, Thomisidae (Kullmann & Zimmermann 1974; Gunderman et al. 1988; Tahiri et al. 1989; Henschel 1990, Evans et al. 1995).

Although Shine (1978) and Sargent et al. (1987) do not explicitly consider the case of extended parental care, their ideas may be applicable to it. Thus, the "safe-harbor" hypothesis (Shine 1978) would predict that the strategy of extended brood care and small egg size may be adaptive if predation pressure is higher in the egg stage than in the hatchling stage. Testing the "safe harbor" hypothesis requires a comparative approach; however, qualitative predictions derived from this theoretical framework can be applied to a single species to ask whether differential predation pressure is at all likely to be an explanation for the unusual resource allocation by the desert spider *Stegodyphus lineatus*. Predation pressure would not be a likely explanation for small egg size if the hatchling stage is at greater risk than the egg stage. A natural population of *S. lineatus* was monitored over their entire reproductive season in order to assess risks and causes of mortality during different reproductive stages. I attempted to determine whether predation pressure differs for the egg stage and the hatchling stage.

METHODS

Study animals.—*Stegodyphus lineatus*, a sedentary spider, builds a retreat in the form of a silk tube; and the web radiates from the entrance of the tube to the nearby vegetation. The size and form of the web depends on vegetation structure and the size of the spider (Ward & Lubin 1993). The average body length of adult females at egg laying in the Negev population was 13.42 mm (SD = 1.44, n = 278). Each female produces a single clutch, and will produce a second clutch only if the first is lost. Egg number is a function of female body mass and varies between 40–140 (mean = 70, n = 53) eggs per clutch. This study started at the end of the mating season when some males were still wandering around in search of mates or cohabiting with females. Voucher specimen of the species are in the National Collection of Israel.

Study site.—The study site was a wadi (dry riverbed) of about 3 km length located on the Avdat plateau, Negev Desert, Israel. The wadi was in a Bedouin grazing area; and goats, sheep, donkeys, and camels foraged in the area every day. Spider densities were higher in the wadi bed than on the slopes. Webs were patchily distributed on shrubs or dry annual vegetation with densities up to 20 webs per 25 m².

Monitoring.—During the first half of May 1993, I marked the nests of 327 female *S. lineatus*. It was not possible to find and mark all spider nests that occurred in the wadi during the first days, and several were over-

looked. These nests were marked on the day first encountered and were included in the sample from then on. Adult females usually do not leave their nests, and females with eggs or young never do so. Only 12 times did I find a female with a new tube. It is possible to distinguish old from new webs by the size of the tube and the occurrence of plant material incorporated in the silk. As a consequence of the continued marking of some webs, sample sizes changed during the observation period. Therefore, daily survival rates were calculated relative to the number of spiders on the previous day. Mortality at day "x" was expressed as the percentage of dead spiders relative to the number of spiders at day "$x - 1$". Daily survival probabilities were calculated by $1 - (mortality/100)$. Daily probabilities were multiplied to obtain the cumulative survival probability function.

Definitions of developmental stages in spiders vary considerably in the literature. I will refer to the egg developmental period as the time from laying until hatching from the cocoon. The hatchling period starts when the young leave the egg sac and ends at the day they start to disperse. The survival probabilities in the egg period and the hatchling period were calculated relative to the total number of females with eggs ($n = 278$) or young ($n = 127$), respectively. The day of egg laying or hatching was set as Day 1 in each case.

Each tube was checked daily at dawn. I recorded whether the females had egg sacs or hatched spiderlings. I also documented whether females had died or disappeared and, if known, the cause of death. The four main predators can be identified by indirect or direct methods. The parasitic wasp *Pseudopompilus humboldti* Dahlbom 1845 deposits an egg on the abdomen of the adult female spider and leaves the spider in the entrance of the nest (Ward & Henschel 1992). The main spider predator, *Poecilochroa senilis* O.P.-Cambridge 1872 (Gnaphosidae), usually stays in the nest feeding on the host for several days. Ant attacks could often be observed or they were identified by the large number of dead ants in the web, and bird or rodent predation always resulted in removal of the whole nest. The same data were recorded to quantify mortality of egg sacs or spiderlings. I never found any evidence for egg sacs being parasitized. Each time an egg sac hatched, measurements
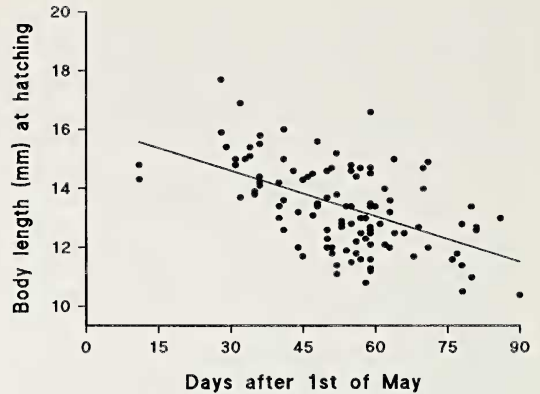

Figure 1.—Relation of female size (body length in mm) at hatching of young and the hatching date, given in number of days after the first day of May.

of the female's body length, prosoma width and opisthosoma width were taken and the number of hatched spiderlings was estimated as exactly as possible without having to destroy the nest. Spiderlings were counted again 25 days after they had emerged from the egg sac. Spiders were measured in an acrylic plastic ("Plexiglas") tube covered on one end with translucent plastic wrap. The spider was fixed against the plastic wrap with an additional inner tube covered with soft foam-rubber. Using a pair of calipers, body parameters were measured to the closest 0.1 mm with an error of 0.2 mm (maximal 5%), estimated from repeated measurements.

RESULTS

At the beginning of the study period (2 May 1993) 2% of 327 females had already laid eggs. The relative number of females with eggs increased every day, and after four weeks 80% of all marked females had reproduced. Some spiders did not reproduce. The average duration of egg development was 30 days (SD = 4, $n = 108$). Early reproducing females were larger than females that laid eggs later in the season ($r^2 = 0.27$, $P < 0.001$, $y = -0.05x + 16.14$) (Fig. 1).

The survival function of all adult females regardless of their reproductive state (in the study area over a period of three months) is shown in Fig. 2. Daily survival rates were similar throughout the reproductive season. Thus, the faster a female can complete reproduction, the lower her risk of dying from pre-
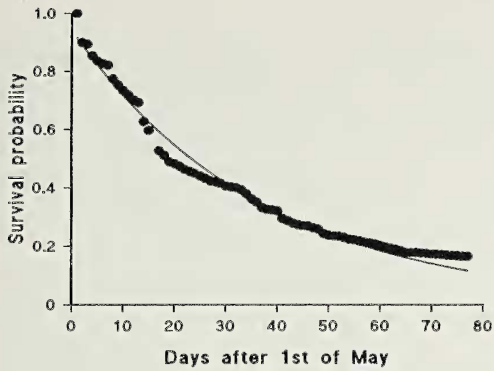
Figure 2.—Cumulative probability of survival of the Negev population over the reproductive period lasting from the first day of May to middle of July; curve fit: $A * e^{(-k * x)}$, $A = 0.94$, $k = 0.027$; $r^2 = 0.98$.
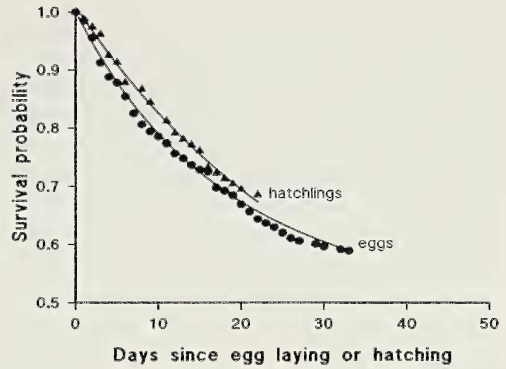

Figure 3.—Comparison of the survival probability during the egg period (circles) and the hatchling period (triangles). Both curves are fitted by the same log logistic functions: $A -\ln (1 + B * e^{(-k * x)})$, for the egg period ($r^2 = 0.996$), $k = 0.043$, $B = -0.401$, $A = 0.488$; and for hatchling period ($r^2 = 0.995$), $k = 0.019$, $B = -0.543$, $A = 0.227$.

dation. However, the curve is flatter at the end when many broods have hatched.

Rates and causes of mortality during the egg development period.—Since reproduction was not synchronous, the day of egg laying was set as Day 1 (Fig. 3) in order to compare the survival of females in different states of reproduction. The figure shows only the mortality of females, not the eggs, because the young depend completely on their mother whereas females can re-lay if they lose a clutch. Of 278 females which produced first egg sacs, 63 lost them, mainly due to predation of egg sacs by ants or males of *S. lineatus* (unpubl. data). Nine females lost their first and second clutch, two lost three clutches and one lost four. Overall, 63 females lost 79 egg sacs. If a spider lost her first clutch, she lost, on average, 20 days (SD = 7.5, $n = 59$) which is the sum of the mean age of the lost eggs plus the mean of 11.6 days (SD = 4.4, $n = 59$) that it took to produce a replacement clutch. This time loss corresponds to a decrease in survival probability of about 15% (Fig. 2). Eight females died before they could produce a second clutch. Fifty-five females laid a replacement clutch but only 16 survived until their young hatched.

Of 278 females with egg sacs, 145 (52.16%) died during the development of their eggs and an additional six never produced an egg sac that hatched. If the female died but the egg sac stayed intact, she still had no reproductive success because spiderlings are not able to leave the egg sac without the help of the

mother. In total 169 females (61%) were attacked by predators at least once during the egg development stage. Sixty-three lost only their eggs and had another chance to reproduce. Some of these females were attacked again with lethal consequences: 59 females were attacked at least twice. In total, 224 predator attacks were counted.

Largely due to predation during the period of egg development, 54.3% (145 dead + 6 unsuccessful) of all females had no reproductive success. The parasitic wasp *Pseudopompilus humboldtii* parasitized 39 females (i.e., 14% of the population of females with eggs). Other predators were birds ($n = 32$, 11.5%), ants ($n = 16$, 5.7%) and spiders (Gnaphosidae) ($n = 10$, 3.6%). The predator was not identified in 48 (17.3%) of the cases of female mortality. In total, 127 (45.7%) females survived until their young hatched.

Mortality during the hatchling period.—Young hatched from clutches of 127 females. Of these, 88 broods (69.3%), with an average of 13.1 (SD = 7.9) dispersing young, survived until the young reached an age of 25 days. Predators attacked 64% ($n = 81$) of all broods; however, only 48% ($n = 39$) of these attacks had fatal consequences in which all the young and the female (if she was not yet eaten by the young) died. In 52% ($n = 42$) of all attacks at least some of the spiderlings survived, for example, by moving into the web during the attack. Initial average brood size was 22

(underestimated because not all spiderlings can be seen without destruction of the nest); and in the attacked broods with survivors, a median of nine spiderlings dispersed. Most of these attacks occurred after the female had died, or if the female was still alive she fell victim, too. In four cases, females lost all their young shortly after hatching. None of these four females lived long enough to complete a second reproductive event, and two made a replacement clutch but died before these young hatched. Of 127 nests with young, 31.5% were attacked by spiders, 21.3% by ants, 5.5% by birds, and 5.5% by unknown predators. The main predator in the hatchling period was the spider *Poecilochroa senilis* which was responsible for 49.3% ($n = 40$) of all attacks.

Comparison of the two periods.—The survivorship functions of the two periods differ in their slopes. Survival probabilities are higher during the hatchling period than during the egg period (Fig. 3). Survivorship for the first 25 days of each period was compared using the method recommended by Hutchings, Booth & Waite (1991). The actual number of animals that died each day is compared to an expected number of dead animals for each day (derived by assuming an even probability of death for animals in both samples). The result gives a χ^2 value of 16.88 ($df = 1$, $P < 0.001$); thus, the hypothesis that mortality rates were the same in both phases is rejected. A χ^2 test using the actual number of spiders that died over the two periods gives the same result as the above method. During the egg period 54.3% (151 of 278, including 6 females that never reproduced successfully) of all females had no reproductive success compared to 30.7% (39 of 127) of the females in the hatchling period ($\chi^2 = 16.9$, $df = 1$, $P = 0.0001$). During the egg period, females suffered a 14% risk of becoming parasitized by the wasp *P. humboldti*. This wasp never parasitizes females with young, presumably because the spiderlings would feed on the female even if she is paralyzed and would therefore kill the wasp larva, too. This might explain a part of the 23.6% lower mortality rate during the hatchling period. Although a high percentage of nests was attacked during the hatchling period ($n = 81$ and 63.8%, compared to 61% and $n = 169$ during egg period), many of the attacks did not result in death of the whole

brood. This is because spiderlings are mobile so that often some young could escape an attack, whereas the entire clutch is lost if the egg sac is opened. Additionally, the young are not able to leave the cocoon without the help of the mother so that they have no chance of survival if the mother dies before hatching.

DISCUSSION

Stegodyphus lineatus females are vulnerable to predation and parasitism. Adult females fall victim to birds, ants, parasitoid wasps, and other spiders. Only 27% of the adult females in the population raised young which successfully dispersed. Of these females, 50% had a reduced reproductive success because predators caused the death of some of the brood. Daily survival probabilities stayed the same throughout the season so that females that reproduce fast have a higher chance of completing reproduction than do females that take longer. Usually, a trade-off between body size and time of reproduction will produce a situation where a female spider reproduces early and small or late and large (Vollrath 1987). In *S. lineatus*, however, large females reproduced earlier than smaller ones although they were all mature at the beginning of the study period. Small females had reduced fecundity because clutch size is a function of body mass in *S. lineatus* (Schneider 1992), and they were also exposed to predation for a longer period of time. Females with high growth rates had the combined advantages of increased fecundity and early reproduction. Spiderlings that hatched early had a high survival probability before dispersal and also more time to feed and grow before prey availability declined in the dry summer.

The significance of body size for the reproductive value of offspring might be one explanation for the high maternal investment in individual offspring. Bigger spiderlings had higher survival probabilities during periods of low prey availability (Schneider 1992), and they may have had an initial foraging advantage with a cumulative effect through time (Schneider 1995). Larger spiders build relatively larger webs, and larger webs catch more prey (Ward & Lubin 1993). Larger spiderlings are more likely to mature early as large adults and therefore have a higher reproductive value. Because of the advantages of early growth for future survival and fecundity, I suggest

that there is selection for small clutches and extended maternal care. Correlations between body size and several traits relevant to fitness, such as mating success for males or time to maturation, are also known for other spider species (Vollrath 1987).

The period of egg development was riskier than the hatchling period, which is in accordance with Shine's (1978) explanation of the evolution of small eggs. If a female survived until her young had left the cocoon, her chances of successfully completing reproduction increased. The wasp *P. humboldti* was responsible for 14% of the mortality in the egg period. In an earlier study in the same area, the rate of parasitism was as high as 25.6% (Ward & Henschel 1992). In general, wasp predation varied between 14–29% depending on the density of the spiders (Schneider 1992; Ward & Henschel 1992; Henschel et al. 1996). Spiders suffered less predation during the hatchling period, both because wasps did not attack during this stage and because attacks by spiders or ants were less fatal then. A possible way of reducing the risk of wasp predation would be to shorten the period of time during which the spiders suffer the highest risk of parasitism: the shorter the interval between molting and egg-laying and the faster a female's eggs hatch, the greater is her probability of survival. Given that all physiological parameters stay constant, a decrease in the amount of yolk decreases egg size and the duration of the egg stage for poikilotherms (Sinervo 1990). A few studies have actually shown that big eggs that are provisioned with a large amount of yolk take longer to develop when compared to smaller eggs with less yolk (reptiles: Sargent et al. 1987; crustaceans: R. Diesel, pers. comm.). A more critical test of this relationship showed that egg development was shortened when the amount of yolk was reduced experimentally, and the young hatched at an earlier stage in their development or at a smaller size (Brestowsky 1968; Sinervo 1990; Sinervo & Licht 1991; Bernardo 1991 and references therein). Further studies are needed to determine whether the relatively low yolk content of *S. lineatus* eggs speeds hatching.

S. lineatus spiderlings are unable to survive without the care of the mother. Their bodies are very soft, almost translucent and without hair. As a result, their abdomen can expand

enormously and growth rates are fast during the period when the females provide food via regurgitation (Schneider 1992). Although the eggs are relatively small in *S. lineatus*, egg development still takes longer than the hatchling period. Eggs seem to develop in a time similar to spiders from other families (such as Theridiidae, Araneidae and Agelenidae) where, depending on the temperature, egg development takes between 10 days (30 °C) and 50 days (10 °C) (Foster & Kingsford 1983; Pulz 1987). The question arises whether the species has reached the lower limit in egg size or whether egg size is a phylogenetic constraint. Data on other species of Eresidae are needed to distinguish between these possibilities and to study the evolution of egg size and maternal care in this group.

LITERATURE CITED

Anderson, J. F. 1990. The size of spider eggs and their energy content. J. Arachnol., 18:73–78.

Bernardo, J. 1991. Manipulating egg size to study maternal effects on offspring traits. Trends Ecol. Evol., 6:1–2.

Brestowsky, M. 1968. Vergleichende Untersuchungen zur Elternbindung von *Tilapia*-Jungfischen (Cichlidae, Pisces). Z. f. Tierpsychol., 25:824–828.

Clutton-Brock, T. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, New Jersey.

Craig, C. L. 1987. The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. American Nat., 129:47–68.

Evans, T. A., E. J. Wallis & M. A. Elgar. 1995. Making a meal of mother. Nature, 376:299.

Foelix, R. F. 1981. The biology of spiders. Harvard Univ. Press. Cambridge, Massachusetts.

Foster, L. & S. Kingsford. 1983. A preliminary study of development in two *Latrodectus* species (Araneae: Theridiidae). New Zealand Entomol., 7:431–438.

Gross, M. R. & R. C. Sargent. 1985. The evolution

of male and female care in fishes. American Zool., 25:807–822.

Gundermann, J. L., A. Horel & B. Krafft. 1988. Maternal food-supply and its regulation in *Coelotes terrestris* (Araneae, Agelenidae). Behaviour, 107:278–296.

Henschel, J. R. 1990. The biology of *Leucorchestris arenicola* (Araneae: Heteropodidae), a burrowing spider of the Namib dunes. Pp. 115–127, *In* Namib ecology: 25 years of Namib research. (M. K Seely, ed.). Transvaal Monograph No. 7, Transvaal Museum, Pretoria.

Henschel, J., J. Schneider, & T. Meikle. 1996. Does group-living or aggregation of the spiders *Stegodyphus* affect parasitism by pompilid wasps? Bull. British Arachnol. Soc., 10:138–140.

Hutchings, M. J., K. D. Booth & S. Waite. 1991. Comparison of survivorship by the logrank test: criticism and alternatives. Ecology, 72:2290–2293.

Kullmann, E. J. & W. Zimmermann. 1974. Regurgitationsfütterung als Bestandteil der Brutfürsorge bei Haubennetz und Röhrenspinnen (Araneae, Theridiidae und Eresidae). Proc. 6th Intern. Arachnol. Cong., Pp. 1125–1146.

Marshall, S. D. & J. L. Gittleman. 1994. Clutch size in spiders: is more better? Funct. Ecol., 8: 118–124.

Pulz, R. 1987. Thermal and water relations. Pp. 26–55, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer Verlag, Berlin Heidelberg.

Roff, D. A. 1992. The evolution of life histories. Theory and Analysis. Chapman & Hall, New York, London.

Sargent, R. C., P. D. Taylor & M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. American Nat., 129:32–46.

Simpson, M. R. 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology, 76:795–800.

Schneider, J. M. 1992. Die Wurzeln des Soziallebens bei der subsozialen Spinne *Stegodyphus lineatus* (Eresidae). Dissertation, Universitaet Muenchen.

Schneider, J. M. 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insect. Soc., 42:237–248.

Shine, D. R. 1978. Propagul size and parental care: The "safe-harbor" hypothesis. J. Theoret. Biol., 75:417–424.

Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution, 44:279–294.

Sinervo, B. & P. Licht. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. Science, 252:1300–1302.

Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford, UK.

Tahiri, A., A. Horel & B. Krafft. 1989. Etude préliminaire sur les intreactions mère-jeunes chez deux espèces d'*Amaurobius* (Araneae, Amaurobiidae). Rev. Arachnol., 8:115–128.

Vollrath, F. 1987. Growth, foraging and reproductive success. Pp. 357–370, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer Verlag, Berlin.

Ward, D. & Y. Lubin. 1993. Habitat selection and the life-history of a desert spider, *Stegodyphus lineatus* (Eresidae). J. Anim. Ecol., 62:353–363.

Ward, D. & J. R. Henschel. 1992. Experimental evidence that a desert parasitoid keeps its host cool. Ethology, 92:135–142.